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SOCIAL LIFE AMONG THE INSECTS[1]

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LECTURE III. PART 2. BEES SOLITARY AND SOCIAL

The Meliponinæ, or stingless bees, are a very peculiar group of nearly 250 species, all confined to warm countries. Fully four fifths of the species occur only in the American tropics and only about one fifth in the Ethiopian, Indomalayan and Australian regions. All the Old World and the majority of the Neotropical forms belong to the genus Trigona; the remainder of the American species are placed in a separate genus, Melipona. The stingless bees are much less hairy and much smaller than the bumble-bees. Some of the species of Trigona measure less than 3 mm. in length and are therefore among the smallest of bees. The colonies vary greatly in population in different species. According to H. von Ihering, those of Melipona may comprise from 500 to 4,000, those of Trigona from 300 to 80,000 individuals. The name stingless as applied to these insects is not strictly accurate, because a vestigial sting is present. It is useless for defence, however, so that many of the species are quite harmless and are called "angelitos" by the Latin-Americans. But some forms are anything but little angels. When disturbed they swarm at the intruder, bury themselves in his hair, eye-brows and beard, if he has one, and buzz about with a peculiarly annoying, twisting movement. Others prefer to fly into the eyes, ears and nostrils, others have a *penchant* for crawling over the face and hands and feeding on the perspiration, or bite unpleasantly, and a few species spread a caustic secretion over the skin. On one occasion in Guatemala large patches of epidermis were thus burned off from my face by a small swarm of *Trigona flaveola.*

There are three morphologically distinct castes. The queen differs from the worker in the smaller head, much more voluminous abdomen, more abundant pilosity, and in the form of the hind legs, the tibiæ of which are reduced in width and furnished with bristles also on their external surfaces, while the metatarsi are elongate, rounded and apically narrowed. The worker, therefore, really represents the typical female of the species morphologically, except that she is sterile, whereas the queen, except in her ovaries, exhibits a degeneration of the typical secondary characters of her sex. There is only one mother queen in a colony, but a number of young daughter queens are tolerated. New colonies are formed by swarming, that is, by single young queens leaving the colony from time to time, accompanied by detachments of workers, to found new nests. The body of the old queen is so obese and heavy with eggs and her wings are so weak that she can not leave the nest after it is once established.

The nests of the Meliponinæ are extremely diverse in structure. They are usually in hollow tree-trunks or branches, less frequently in walls. Some of the species nest in the ground, and a few (*T. kohli, fulviventris, crassipes, etc.,*) actually build in the centers

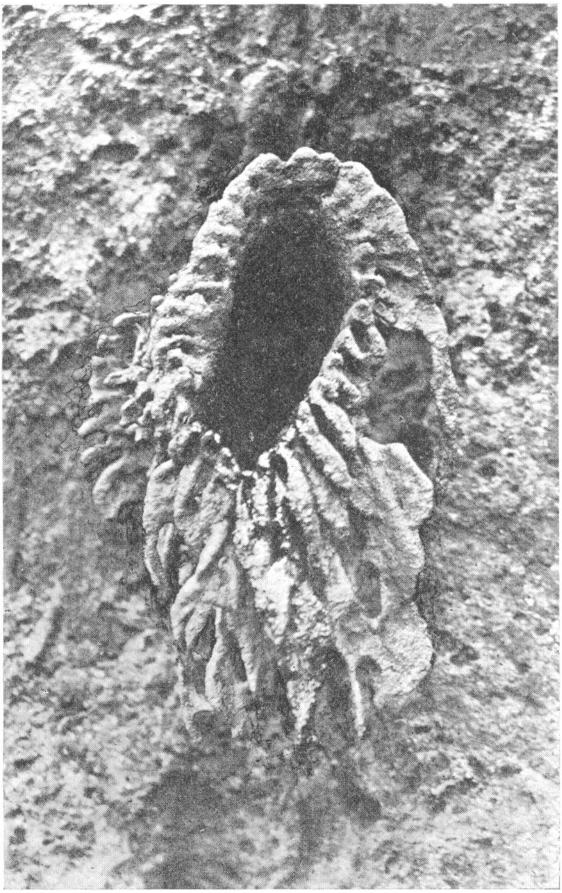

FIG. 46

Cerumen spout, or nest entrance of a large colony of *Trigona heideri* Friese nesting in a hollow tree at Kartabo, British Guiana. About 1/3 natural size. Photograph by Mr. John Tee Van.

of termite nests. The nest is made of wax, which most of the species mix with earth, resin or other substances, so that it is chocolate brown or black and is called "cerumen." The wax is secreted only between the dorsal segments of the abdomen, and is produced by the males as well as by the workers—the one case in which a male Hymenopteran seems to perform a useful social function. The workers not only collect nectar and pollen but they seem to have a greater propensity than other social bees for gathering propolis, resins and all kinds of gums and sticky plant-exudations. And unlike other bees they are also fond of visiting offal and the feces of animals. One species is said even to eat meat (*T. argentata,* according to Ducke).

The entrance to the nest may be a simple hole, but more often it is a projecting cerumen spout or funnel, which differs considerably in different species (Fig. 46). In some East Indian Trigonas its lips are kept covered with sticky propolis to prevent the ingress of ants and other intruders (Fig. 47*AB*). In most of the South American species its orifice is guarded during the day by

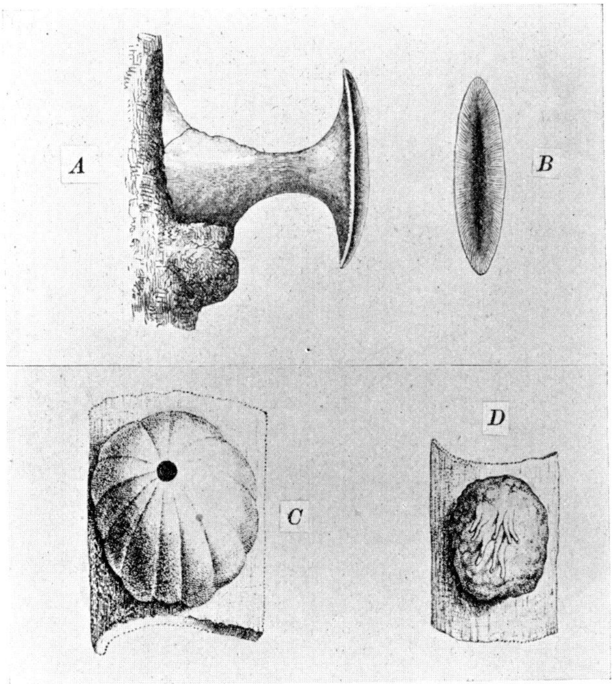

FIG. 47

Cerumen entrances to nests of Meliponine bees. *A.* Of *Trigona laeviceps* of India in profile; *B,* same seen from the front (After C. S. P. Parish); *C,* nest entrance of *Melipona quinquefasciata*; *D,* nest entrance of *Trigona limao* After F. Silvestri.

a special detachment of workers and is closed at night with a cerumen plate or screen. The interior of the nest presents a peculiar appearance. If it is in a hollow tree-trunk or branch the cavity is closed off at each end by a thick lump or plate of cerumen (the "batumen"). The nest proper (Figs. 48 and 49), constructed in the tubular space thus preempted, consists of two parts, one for the brood and one for the storage of various foods and building materials. The brood portion consists typically of a hollow spheroidal

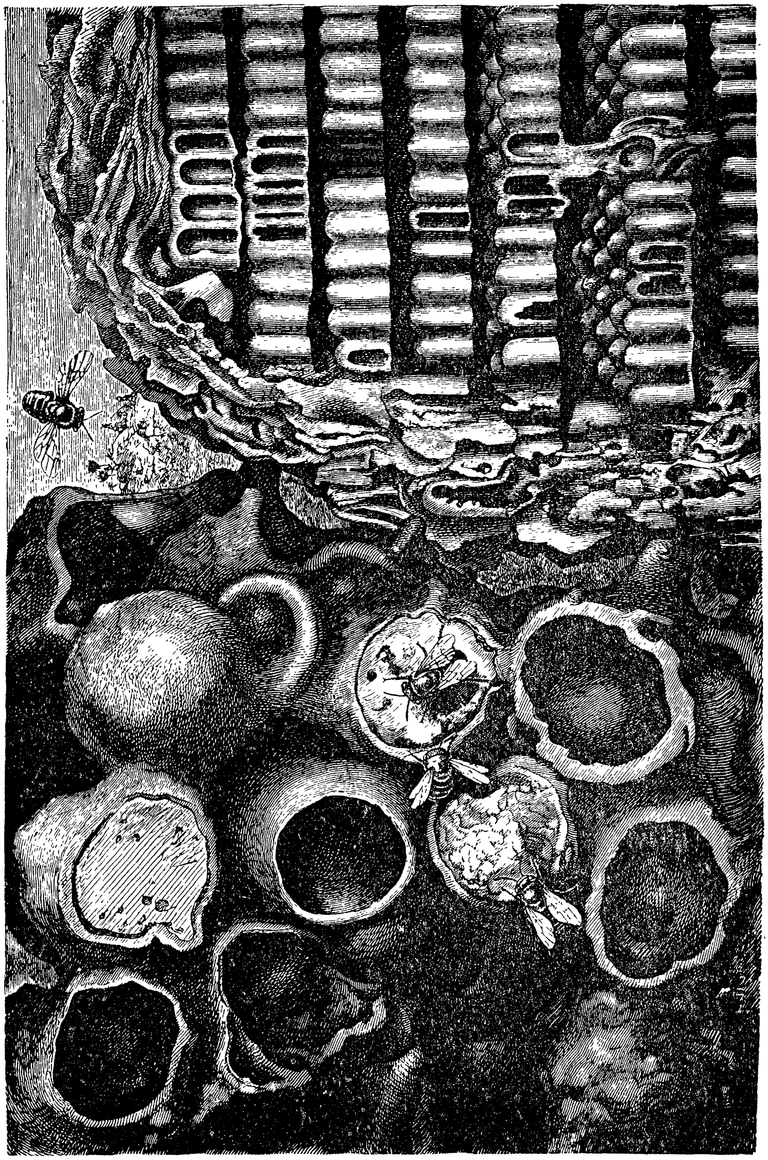

FIG. 48

Portion of nest of *Melipona scutellaris*, showing brood-comb (to the right) and the large honey pots and pollen pots (to the left). Subdiagrammatic drawing from Emile Blanchard.

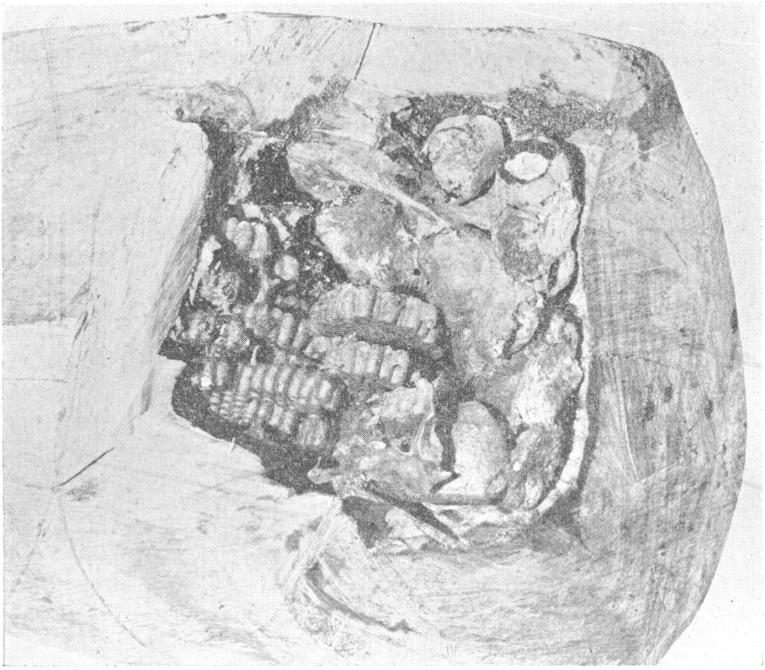

FIG. 49
Nest of Melipona sp. in hollow log, showing brood-comb (to the left), pollen pots and honey pots (to the right). Photograph by Dr. E. F. Phillips. About one half natural size.

envelope of irregular, interconnected cerumen laminæ, forming the walls of an elaborate system of anastomosing passage-ways and enclosing a large central space occupied by a series of combs of hexagonal cells. There is only one layer of cells in each comb and they all open upwards, not downwards as in the social wasps. In some species the combs are regular and disc- or ring-shaped structures, in others they are arranged in a spiral or more irregularly. Their cells are used exclusively for rearing the brood. In Melipona and some species of Trigona they are all of the same size, but in several South American species of the latter genus single larger cells are constructed, especially towards the periphery of the combs, for the rearing of queen larvæ. All this elaborate arrangement would seem to be a preparation for a very specialized system of caring for the young, but such is not the case. The workers, precisely as if they were solitary bees, put a quantity of pollen and honey into each cell, and after the queen has laid an egg in it, provide it with a waxen cover, so that the larva is reared exactly like that of a solitary bee. There is mass but not progressive provisioning and the adult bees do not come in contact with the growing larvæ. The queen-cells are treated in the same manner, the only difference being that they are provided with a greater amount of pollen and honey. Among the species whose queen cells are no larger than those in which the workers and males are reared, the queens emerge with small ovaries and develop them later, but among the species which build large cells for the queens, the latter emerge with the ovaries fully developed. These differences are of considerable interest in connection with the queen honey-bee.

Outside the cerumen involucre enclosing the brood combs the workers construct large elliptical or spherical pots, some for the storage of honey, others for pollen and in some species still others

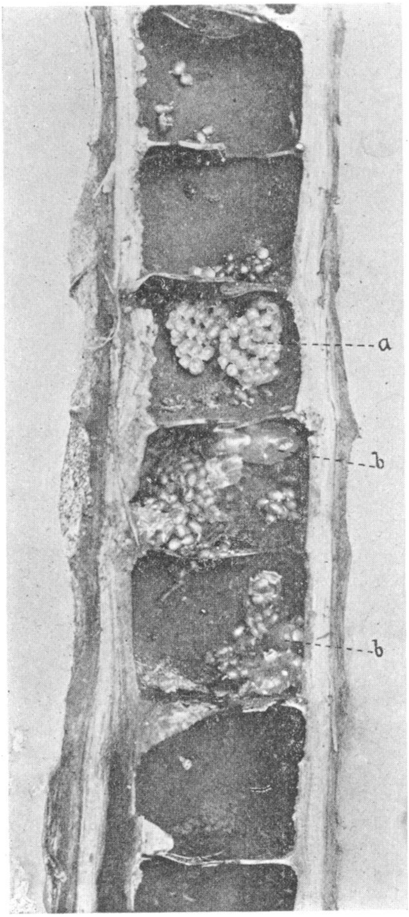

FIG. 50
Nest of a small Trigona (worker only 2.5 mm. long!) representing a new species near *T. goeldiana* Friese, in the hollow internodes of a small *Cecropia angulata* Bailey (sp. nov.) at Kartabo, British Guiana. *a*, brood-cells containing adult larvæ and pupæ; b, honey pots. Slightly enlarged. Photograph by Mr. John Tee Van.

for propolis. In one species (*T. silvestrii*) the pollen-pots are long and cylindrical while the honey-pots are small and spherical. This same arrangement is known to occur also in one of the European bumble-bees (*B. pomorum*). The Meliponinæ may also store other substances in the outer portions of their nests. In one nest of a black Trigona, which I observed at Kalacoon, in British Guiana, there were several lumps, each weighing 10 to 20 grams, of a hard substance closely resembling sealing wax in color and consistency. The species which build their nests freely on the branches of trees cover them with protective layers of cerumen arranged like those surrounding the brood combs.

The Old World Trigonas (*canifrons,* according to W. A. Schulz) and some of the South American species (*timida, silvestrii* and *cilipes,* according to Silvestri; *silvestrii* and *muelleri,* according to H. von Ihering; and a very small undescribed species allied to *T. goeldiana,* which I found in British Guiana, represent a more primitive stage in the construction of the nest (Fig. 50). The brood cells in these forms are elliptical and are not arranged in a comb but are isolated or loosely connected with one another by delicate waxen beams, or trabeculæ. They are therefore essentially like the cells of bumble-bees and solitary bees. It should be noted also that the Meliponinæ, like the bumble-bees, tear down their cells after they have been used and construct new ones in their places.

The rearing of the brood of all the castes in closed cells, after the manner of the solitary bees, is very significant, since it is the only case among the social Hymenoptera of a complete lack of contact between the adults and the larvæ. Even the bumble-bees open their cells from time to time and feed the older larvæ, and among the honey-bees the cells remain open throughout larval development. It is obvious that the Meliponinæ have either retained unaltered the ancient method of rearing the young in closed cells, employed by all the solitary bees, or have reverted to it after practicing a method more like that of the bumble-bees or honey-bees. As there seem to be no cogent reasons for adopting the latter alternative, I am inclined to believe that the former is the more probable and that unlike the wasps these highly social bees have never passed through a stage of actual trophallactic contact between mother and offspring. After considering the honey-bees I shall return to this question.

The Apinæ, or honey-bees, are separated by a wide gap from the Meliponinæ and Bombinæ and their origin is still wrapped in obscurity. Certain species, referred by their authors to the genus Apis, are recorded from the European Miocene (*A. adamitica*), Baltic Amber and Upper Oligocene (*A. meliponoides* and *hen-*

shawi). The genus as it exists to-day comprises only four species: *dorsata, florea, indica* and *mellifica,* the common honey-bee of our apiaries. *A. indica* and *mellifica* are so very similar in structure and habits and hybridize so readily that both Friese and von Buttel-Reepen have regarded the former as a mere race, or subspecies of the latter. Von Buttel-Reepen, however, has recently raised *indica* to specific rank on what seem to me to be rather dubious grounds. Inasmuch as *dorsata, florea* and *indica* are confined to the Indomalayan region, it has been usually assumed that *mellifica,* though now cosmopolitan, is also of South Asiatic origin. But von Buttel-Reepen believes that it had its origin in Germany and bases his opinion on the existence of the above-mentioned fossils in Germany and on the fact that the true *mellifica* did not exist in India till it was introduced by Europeans. The bee originally kept in that country by the natives was *indica.* The eminent melittologist's view is so startling that one is tempted to suppose that he, like some other German investigators, is the victim of a desire to make his fatherland the source of all good things. The following considerations seem to me to leave little ground for his opinion: First, if *mellifica* was not originally present in India it is probably because *indica* happens to be the South Asiatic race of the species. Second, the type of *mellifica,* that is, the form to which Linnaeus first gave the name, is, of course, the dark German, or northern race, and it is natural to regard the many local races and varieties in other parts of Europe, in Africa and Asia as mere modifications of the German type. But such a procedure is unwarranted in phylogeny, since the selection of the German race as the specific type was a mere taxonomic accident. Had a Hindoo entomologist preceded Linnaeus, *indica* would be the type of the species, and the Hindoo, aware of the existence of two other species of Apis in his and neighboring countries and nowhere else, would properly regard the genus as of South Asiatic origin and the species *indica* as having spread to Europe and Africa and as having produced among others a dark Germanic race. Third, it is by no means certain that the fossil forms, which have been described from imperfect specimens, really belong to Apis or that they are in the direct line of descent to that genus. And even if we admit this to be the case, it does not follow that they must have originated in Germany. Fourth, granting that a race of *mellifica* existed in that country during the Miocene, it must either have become extinct during the Ice Age or have been driven into Southern Europe. That this identical race and not a new one arising from southern forms later returned to Germany is a pure supposition. Fifth, the tropical origin of the honey-bee is indicated by its in-ability to form new colonies except by swarming, precisely like the tropical Meliponinæ and Vespidæ. And while it is true that the climate of Central Europe during the Oligocene and Miocene was tropical or subtropical, the existence at the present time of at least three distinct species of Apis in the Indomalayan region and nowhere else makes it seem much more probable that the ancestors of *mellifica* emigrated from Asia into Europe than in the reverse direction, especially as Southern Asia is a well-known center from which many other animals have been distributed. The spread of the honey-bee throughout the world is evidently due to its extraordinary adaptability to the most diverse flowers and to a great range of temperature, to its habit of storing large quantities of honey and its ability to maintain a rather high temperature in the hive during periods of cold weather. This unusual plasticity is peculiar to the species and is not the result of domestication. The insect, in fact, has never been domesticated.

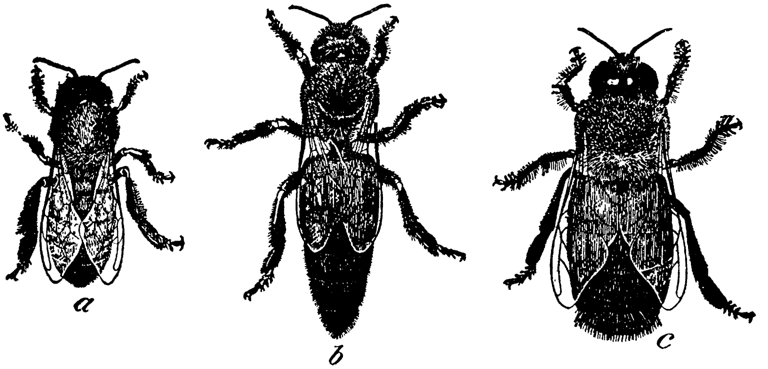

FIG. 51
Honey-bee (*Apis-mellifica*), *a,* worker; *b,* queen; *c,* male (drone). Twice natural size. After E. F. Phillips.

Like the Meliponinæ the species of Apis have three well-developed castes (Fig. 51). Normally there is only a single queen in the colony and she will not tolerate the presence even of another young queen. Swarming takes place by the old queen leaving the colony accompanied by a large detachment of workers when a young queen is about to emerge from her cell, and if several young queens are to emerge in succession, the older leaves before the next appears. It will be noticed that this is different from the swarming of the Meliponinæ, since in these bees the old queen remains in the nest and the young queens accompany the swarms of workers. When the queen's eggs are fertilized they develop into workers or queens according to the way the larvæ are fed, but when unfertilized into males or drones, as is also the case with the eggs that are sometimes laid by workers. All the species of Apis make pendent combs of pure wax, which is secreted only by the workers and only between the ventral segments of the abdomen. The combs differ from those of the Meliponinæ and wasps in consisting of two layers of hexagonal cells, and the brood cells remain open throughout larval development, the young being fed progressively. The three species of Apis represent as many different phylogenetic stages, which may be briefly described.

A. dorsata is the largest and most primitive form (worker 16-18 mm.; queen 23 mm.; drone 15-16 mm.). It builds from the lower surface of a branch a single large semicircular comb, sometimes with a superficial area of a square meter. Its cells are regularly hexagonal and all alike. Part of them are used for storing honey, the remainder for the brood. In this species, therefore, the workers, queens and drones are all reared in cells of the same size and shape, like the species of Melipona and many Trigonas. *A. dorsata* is a nomadic bee, which builds its comb where flowers are abundant and after they have ceased to bloom deserts the structure and builds a new one in fresh pastures. Owing to this habit, all the attempts that have been made both in Europe and the United States to establish this bee in apiaries have failed.

A. florea is the smallest species in the genus (worker 7-8 mm.; queen 13-14 mm.; drone 12 mm.) and in certain respects represents an interesting transition between *dorsata* and *mellifica*. The drone is peculiar in having a finger-shaped process on the inner border of the hind metatarsus. Like *dorsata, florea* makes a single pendent comb, but it is much smaller and narrower and consists of four different kinds of cells. At the base where the comb surrounds the supporting branch the cells are hexagonal, large and deep and are used for storing honey. Below these there is a broad zone of small hexagonal cells for the worker brood and at the apical fourth still larger hexagonal cells for the drone brood. Finally, attached to the free border and depending like stalagtites there are several long conical cells for the queen larvæ.

A. mellifica and its subspecies *indica*, etc., differ from *dorsata* and *florea* in nesting in hollow cavities (tree-trunks, caverns, hives) and in constructing several pendent combs side by side, each presenting the types of cells seen in *florea*, except that there is no special type for storage, the honey being kept in cells like those used for rearing the worker brood. Moreover, the queen cells are never built on drone but only on worker comb. The singular shape of the queen cells (Fig. 52), so very different from the hexagonal cells, and the fact that they are the only cells torn down by the workers after being used, indicate that they are archaic

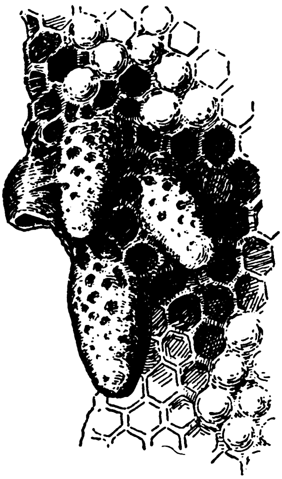

FIG. 52
Queen-cells of the honey-bee. Natural size. After E. F. Phillips.

structures of considerable phylogenetic significance. They are, indeed, reminiscent of the only type of cell constructed by the bumble-bees. But owing to the fact that conical queen cells occur only in *A. florea* and *mellifica* and are the same in both species we are unable to advance any reasons for their retention among cells of the highly specialized hexagonal type. On rare occasions

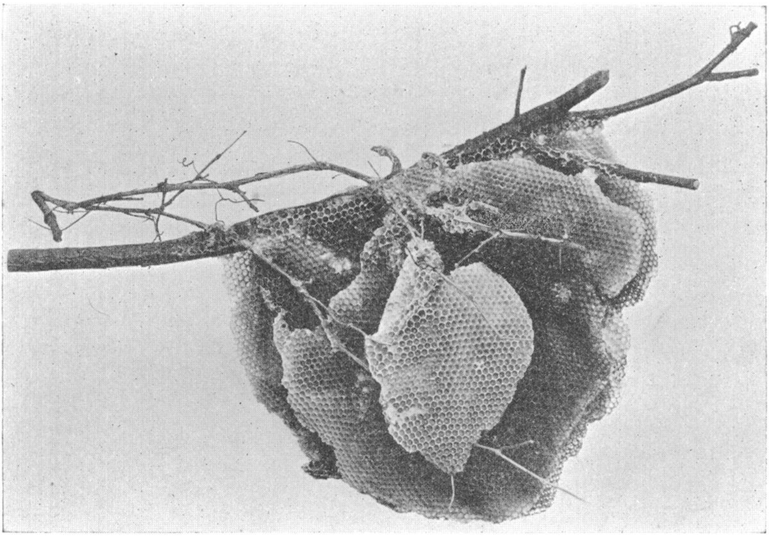

FIG. 53
Comb built by a colony of honey-bees on the branches of a tree. From a specimen in the American Museum of Natural History by which this photograph and Fig. 54 were contributed.

a swarm of honey-bees, failing to find a hive or hollow tree-trunk, will construct its comb among the branches of trees or bushes. Such exposed nests have been described by Bouvier, and there is an unusually fine example in the American Museum of Natural History (Figs. 53 and 54). It will be noticed that in form each comb resembles the single comb of *A. dorsata* or *florea*.

Except in the development of her ovaries, the queen honey-bee is a degenerate female, a mere egg-laying machine, entirely dependent on her worker progeny. The pollen-collecting apparatus of the hind legs, so well developed in the worker and so charac-

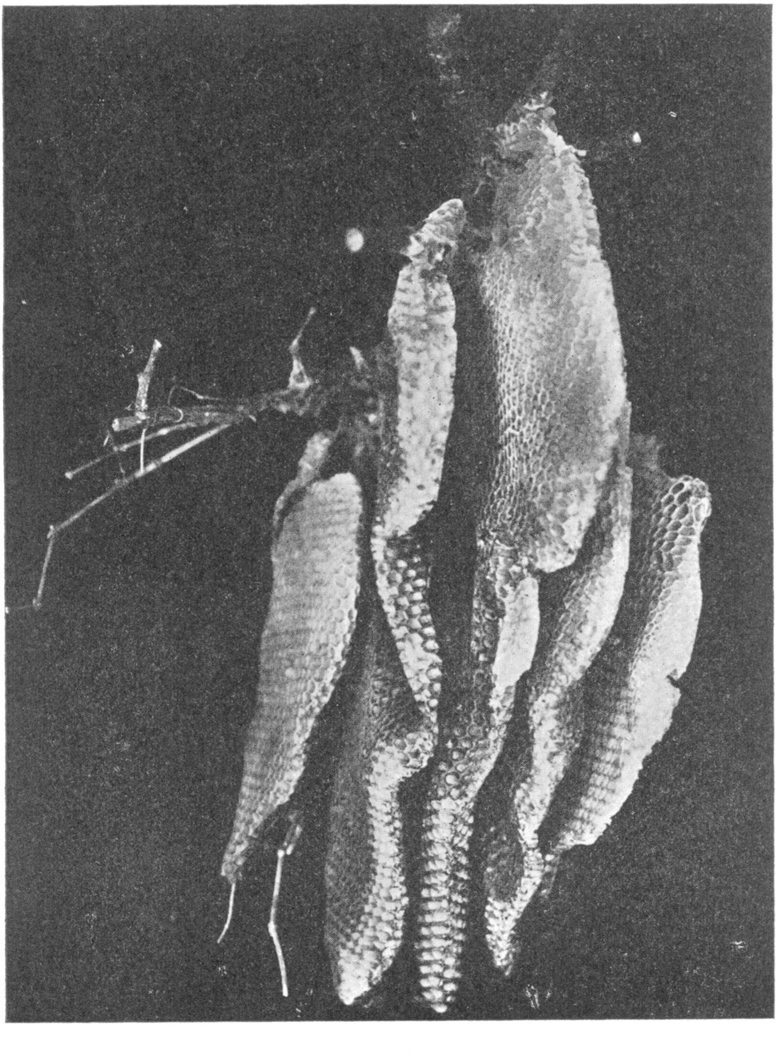

FIG. 54
Same comb as shown in Fig. 53, seen from the end.

teristic of the females of all non-parasitic, podilegous bees and of the queens of the bumble-bees, is undeveloped, her tongue and sting are shortened, her brain is smaller and she lacks the pharyngeal salivary glands of the worker. That these differences are due to larval feeding is proved by the experiment of transferring eggs and very young larvæ from worker to queen cells and *vice versa.* Transferring eggs from drone to worker or queen cells does not, however, alter the sex of the insect reared, since it develops from an unfertilized egg. Under normal conditions the time required for the development and the chemical composition of the food administered to the larvæ differ for the three castes. The difference in the rate of development is shown in the following table from von Buttel-Reepen:

DURATION OF DEVELOPMENT IN THE HONEY-BEE
(After von Buttel-Reepen)

DEVELOPMENT OF THE BROOD	QUEEN (DAYS)	WORKER (DAYS)	DRONE (DAYS)
Duration of egg (embryonic) development	3	3	3
Duration of larval development	6	6	6
Duration of spinning and resting period	2	4	7
Change of pupa to imago	5	8	8
Total	16	21	24

The composition of the food, which, for the queens and the earliest stages of the workers and drones, is a secretion ("royal jelly") of the pharyngeal glands of the worker nurses, is shown in von Planta's table taken from the same author:

COMPOSITION OF LARVAL FOODS OF THE HONEY-BEE
(After von Planta)

PERCENTAGES OF DRIED SUBSTANCE	QUEEN LARVÆ (AVERAGE)	DRONE LARVÆ UNDER 4 DAYS	DRONE LARVÆ OVER 4 DAYS	DRONE LARVÆ AVERAGE	WORKER LARVÆ UNDER 4 DAYS	WORKER LARVÆ OVER 4 DAYS	WORKER LARVÆ AVERAGE
Proteid	43.14	55.91	31.67	43.79	53.38	27.87	40.62
Fat	13.55	11.90	4.74	8.32	8.38	3.69	6.03
Sugar	20.39	9.57	38.49	24.03	18.09	44.93	31.51

We see from these tables that the queen, although the largest of the three castes, reaches maturity in about 16 days. She is fed only on "royal jelly," without admixture of honey or pollen. These highly nutritious rations (43.14 per cent. proteid) are undoubtedly responsible for her very rapid growth. The worker is given pollen and honey after the fourth day and requires 21 days to complete her development. The feeding of the drone is similar, but he receives less sugar and more fat and his development is protracted to 24 days.

The foregoing considerations suffice to show the complexity of the whole matter of sex-determination and caste-differentiation in the honey-bee. There are libraries of contentious discussion of these subjects, which can not, of course, be adequately treated in a general lecture. Although all competent authorities agree that the drones arise from parthenogenetic or unfertilized eggs and the queens and workers from fertilized eggs, it is impossible, in the present state of our knowledge, to decide between two different theoretical interpretations of the facts. According to one, first stated by Dzierzon and more recently maintained by Weismann and his pupils and especially by von Buttel-Reepen, the queen lays only one kind of egg, which is potentially indifferent but has its sex determined at the moment of fertilization; according to the other, advocated by Beard, von Lenhossek and Oscar Schulze, there are really two different kinds of eggs, one of which does not need to be fertilized and develops into the drone, whereas the other requires fertilization to be viable and develops into a queen or a worker. Normally the queen lays unfertilized eggs only in the large drone cells and fertilized eggs only in the small worker cells and the peculiar conical queen cells. The hypothesis that the difference in the width of the cells is the stimulus which causes the queen to close or open the duct of her spermatheca and thus prevent or permit the exit of sperm while the egg is passing from the ovaries on its way to being laid, can not be accepted, because the queen often oviposits in cells which have had only their basal portion completed. Moreover, this hypothesis will not apply to the Meliponinæ, which rear males and workers in closed cells of the same size or to cases like those of the solitary wasps described in the preceding lecture and many solitary bees which regulate the size of the cell and the amount of provisions according to the sex of the offspring. These peculiar phenomena, first observed by Fabre in Osmia, Halictus and Chalicodoma, have been recently confirmed by Verhöff, Höppner and Armbruster. The observations show that the female bee must be aware of differences between her eggs sometime before she begins to lay them and certainly before there are any such stimuli as contact of her abdomen with the walls of the cell.

Referring to the Dzierzon theory, Phillips says: "The facts observed in the apiary on which this belief is based are as follows: (1) If a queen is unable to fly out to mate or is prevented from mating in some way she usually dies but if she does lay eggs, as she may, after three or four weeks, the eggs which develop are all males; (2) if when a queen becomes old her supply of spermatozoa is exhausted, her offspring are all males; (3) if a colony becomes queenless and remains so for a time, some of the workers may begin egg-laying and in this case too only males develop. The author has found that many eggs laid by drone-laying queens fail to hatch and, in fact, are often removed in a short time by the workers. This makes it impossible for us to accept Dzierzon's statement that all eggs laid by such a queen become males and the statement must be modified as follows: all of those eggs laid by a drone-laying queen which develop become males. The potentialities of the eggs which never hatch are not known. In addition to the facts here stated, the theory of the parthenogenetic development of the drone is supported by investigation of the phenomena of development in the egg.'' He becomes more explicit in the following passage: ''If we take into consideration the important fact that not all eggs of an unfertilized (drone-laying) queen hatch, then the bee does not appear as an exception in nature. It seems clear, however, that the statement of Dzierzon that all the eggs in the ovary are male eggs can not be accepted and it is, in fact, not improbable that the eggs destined to be females die for want of fertilization, while the eggs destined to be males, not requiring fertilization, are capable of development. It should be understood that the casting of doubt on Dzierzon's theory of sex determination does not invalidate his theory in so far as it pertains to the development of males from unfertilized eggs.''

There are also several cases of hybridization that seem to indicate that Dzierzon's theory is only a partial or approximate interpretation. When a yellow Italian queen bee mates with a black German drone, the drone offspring, being fatherless, should of course be yellow like the mother, whereas the workers should combine the characters of both their parents. This is often the case, but although von Buttel-Reepen is a staunch supporter of Weismann and adheres rigidly to the Dzierzon theory, he is compelled to admit that occasionally ''when an Italian queen is fecundated by a German drone, numerous blended hybrids (''Mischlinge'') appear during the first year, but during the second year almost exclusively Italian, and in the third year exclusively Italian workers are produced, so that the population must be regarded as purely Italian.'' He has himself witnessed this phenomenon and states that it has also been observed by Dönhoff, Dzierzon and Cori. The only explanation von Buttel-Reepen has to offer is that the sperm, stored in the spermatheca of the queen, may in the course of time be increasingly affected by the secretions of her spermophilous glands, which keep the paternal elements alive during the three to five years of her life. The facts can hardly be explained on Mendelian principles even if we make all due allowance for the impurity of the German and Italian strains that produced the hybrids. It looks as if, at least under certain conditions, workers might develop from unfertilized eggs. According to Onions, the workers of a South African race of honey-bees are able to produce workers parthenogenetically, and Reichenbach, Mrs. A. B. Comstock and Crawley find the same to be true of worker ants of the genus Lasius.

I believe that Phillips, in the remarks above quoted, suggests an important fact which has been too little noticed and may account for much misunderstanding in regard to sex determination in the honey-bee. Accurate knowledge of the life-history of a particular individual in a colony of social insects is almost or quite unattainable, for two reasons: first, the egg can not be isolated and the larva brought up by hand, like a young chick, because it requires the presence of nurses of its own species and they will not rear it under abnormal conditions; and second, the workers of many social insects are very fond of eating the eggs and young larvæ and these same workers or the queen not infrequently at once lay eggs in the place of those devoured. This behavior is especially common and disconcerting among the ants. Now a rigid control would require not only that the mother insect should be observed during the very act of oviposition but that the egg and resulting larva should be kept under constant observation day and night till the completion of development. A relay of observers, changing every few hours for two or three weeks, would therefore be needed in order to make sure that a particular adult had developed from a particular egg, and it would be necessary to observe many individuals in such a manner before we should have the data for accurate conclusions. In fact, we shall need all the resources of a specially equipped laboratory, with a specially trained staff, for any final solution of many of the peculiar developmental problems suggested by the honey-bee and other social insects.

Among these problems we should also have to include that of the differentiation of the two female castes, that is, the problem as to whether the worker and queen arise from one kind or from two different kinds of eggs. The experiments of transferring larvæ of different ages from worker to queen cells, as previously stated, and the existence of series of transitional forms between the worker and the queen, naturally lead to the view that there is only one kind of female egg and that the character of the larval food after the fourth day determines whether the adult is to be a worker or a queen. This may be true of the honey-bee, but, as we shall see, observations on certain ants and termites indicate that there may be more than one kind of female egg.

The main object of the rich and abundant food administered to the larva of the queen honey-bee is evidently the rapid development of her ovaries, so that she may begin to lay eggs very soon after emergence. This is also indicated by the conditions in the Meliponinæ. The Melipona queen, which is reared in a closed cell of the same size as that of the workers and on the same amount of food, emerges with rudimentary ovaries and has to develop them by subsequent feeding during her adult instar, whereas the Trigona queen, which is reared in a large cell with more food than is given to the worker larvæ, emerges with mature or nearly mature eggs in her ovaries. All these queens, however, are distinguished from the cospecific workers by certain degenerate or primitive characters, which, it would seem, must owe their peculiarities either to the indirect, inhibiting or modifying action of chemical substances (enzymes) in their food or to the more direct action of hormones, or internal secretions produced by the developing ovaries. The great size of the ovaries in the queens of all these social bees accounts, of course, for their extraordinary fecundity and the size of their colonies. Cheshire computed the number of eggs which may be laid during her lifetime by a vigorous, fecundated honey-bee queen as about 1,500,000, and, according to von Buttel-Reepen, we should find in her spermatheca no less than 200,000,000 spermatozoa. It is not surprisisng, therefore, that a hive, at the time of its climax development during the early summer, may contain 50,000 to 60,000 or even 70,000 to 80,000 bees.

In conclusion I may refer to one of the negative peculiarities of social bees—the absence of that peculiar interchange of nutriment between the adult and larva, or trophalaxis, which seems to be a powerful factor in integrating and maintaining the colonies of the social wasps. Among the Meliponinæ the food and egg are simply sealed up in the cell, so that there can be no contact between adults and larva, and even the honey-bee worker does not place the food on the mouth of the larva but pours it on the bottom of the cell where it can be imbibed when needed. So far as known, the bee larva, unlike the wasp larva, produces no salivary secretion to attract its nurses, though it might be going too far at the present time to say that this is certainly not the case. It is quite probable, nevertheless, that the sources of the development and perpetuation of adult and larval contact, so essential to the maintenance of social life among the Bombinæ, Meliponinæ and Apinæ, are to be looked for in other directions. Hermann Müller long ago pointed out, as I stated in the preceding lecture, that the transition of the adult wasp from an insect to a nectar and pollen diet was due to economy of food. These latter substances represent a very concentrated and energizing food supply and one that can be more readily obtained in great abundance than insect food. Hence it is not surprising that a large group of insects like the bees has become so exquisitely anthophilous, and that the exploiting of larval secretions is unnecessary. It will be noticed that all three subfamilies of social bees store quantities of pollen and honey in open cells and such easily accessible stores of liquid and very finely divided food make even the reciprocal feeding of the adult workers in bee colonies superfluous. This storage of food may be at least one of the reasons why such exchanges of nutriment as we observed among the social wasps and shall see again in a more exaggerated form among the ants and termites were either never developed or were long ago discontinued by the social bees.